DROSOPHILA IN NEW ENGLAND

By Eliot B. Spiess

INTRODUCTION

With the current growing interest in genetic analysis of natural populations of Drosophila, it has become important to fill in the many gaps in our knowledge of distribution and seasonal fluctuations of the numerous species of the genus. One of the sections of the United States which has most urgently needed collecting heretofore is the northeast.

This section is an interesting one because it lies in the northeastern part of the Transition Life Zone on the eastern edge of the Canadian Life Zone. Conditions are particularly severe in winter, and only a few species of the genus are actually able to survive in the wild state. Just what species these are and what adaptations they possess in order to establish themselves as native wild species are of particular interest. The limits of distribution of these species and those of more southerly distribution throughout the New England region cannot be definitely stated as yet.

MATERIALS AND METHODS OF COLLECTING

Collections were begun in 1946 in an effort to discover good material for genetic studies. The collections cover the seasons of 1946 and 1947. At the end of the second season the genetic work was terminated, but the data obtained from trapping flies should provide for possible future patterns of collecting for any desired cytogenetic analysis.

During the 1946 season two methods of trapping were used, and improvements were made from time to time so that by the 1947 season an efficient scheme was worked out. At first, pint mason pars were used with molasses cornmeal agar food yeasted to attract the flies. However, this trap, which was used during April and May of 1946, proved to be too heavy and bulky. Paper cups and fermenting banana mash were used from then on.

Traps were left out for from three to five days depending on

the drying rate of the food surface. Fresh banana mash was added, or new cups were set out whenever the surface of the bananas became hard or unsatisfactory for collecting.

All specimens were etherized in the field in the following manner: a flat finely meshed net which fitted snugly around the top of a paper cup was used to prevent escape of flies; the cup was turned so that etherized flies would not fall into the sticky banana; ether was applied to the net, and after about thirty seconds the flies could be collected into a vial.

In all cases traps were placed in areas of continuous shade. It was found that most flies in summer occurred in large wooded areas which were somewhat more cool and moist on hot days than open country. Whenever more than one collection was made on one day, it was always observed that more flies were caught toward evening than during the sunny hours of the day. Such behavior agrees with Dobzhansky's observations that *D. pseudoobscura* comes to traps in largest quantities just after sunrise and just before sunset.

THE 1946 BREEDING SEASON

Collecting was started in the Arnold Arboretum, Jamaica Plain, Massachusetts. A great deal of time was spent in developing technique in this locality, so that the data are not as complete as could be desired. Also because the locality was constantly being visited by crowds of sight-seers this was not kept up as a trapping area after early July. The results of this collection and subsequent collections are given in tables at the end of the text.

The writer is very grateful to Mr. Gorden Allen who was kind enough to set out a few traps at North Haven Island, Penobscot Bay, Maine, during the last week in June.

The third collecting locality was Windham township, Vermont, at an elevation of 1800–2000 feet in sugar maple, beech, birch, and conifer forest. Human habitations in this area are very few and were approximately one fourth to one half mile from the trapping locality at the very nearest. Two collections were made, one in late June and early July, the other in early August.

A fourth area was in a woodland in Braintree, Massachusetts, during July, August, and September. This is a residential suburban district where houses are widely separated, and open meadows and small woods are common. Collecting here was done close to fruit trees where the last year's fruit covered the ground and also in the nearby small woodland of oak, birch, and maple.

The last and most rewarding area from the standpoint of numbers of individuals and species was the Gray Herbarium Gardens located in Cambridge, Massachusetts. The gardens occupy an area of about seven acres which before the war had included well-cultivated plots and groves of native and exotic plants, but at present they are untouched and seldom visited by outsiders. The gardens are fenced in and are located near a residential suburban area.

THE 1947 BREEDING SEASON

The Gray Herbarium Gardens site was chosen for the 1947 season's collection, and it was decided that the entire season should be sampled in that area alone to discover which populations undergo significant seasonal fluctuations. In order to get as accurate an estimate as possible of the species' concentrations, sampling was performed in the following manner: fresh food or new traps were put out as needed approximately every three to five days; six traps were continually maintained in the area; and samples were taken on convenient evenings about twice a week (that is, on evenings when there had been no rain nor considerable cloudiness during the afternoon). The temperature and state of the weather were recorded at each collection. Taking the samples just prior to sunset each time should have largely eliminated any variation in numbers coming to the traps owing to diurnal periodicity in activity of the flies.

The weather data included in the table following are from the Boston Weather Station. No significant differences were found between temperature readings at the collecting area and the readings given by the Boston Weather Station.

GEOGRAPHICAL OCCURRENCE OF SPECIES

From a total of about thirty species of *Drosophila* which have been found in or near the New England area (that is, as far

west as Ohio or south to New Jersey) only seventeen species were definitely identified by this writer during 1946–47 from the localities mentioned above. However two species may be added to this number: (1) *D. narragansett* was not distinguished from *D. athabasca* in this work; yet because it is such a rare species, it would not greatly alter the numbers given for *athabasca*. (2) A species in the *quinaria* group was found which is either a subspecies of *D. subquinaria* or possibly a new species.

Subgenus *Hirtodrosophila*

No members of this subgenus were found, although *D. duncani* and *D. chagrinensis* have been reported in the past from eastern Ohio.

Subgenus *Dorsilopha*

D. busckii was found in small quantities in Cambridge, Mass., during July, 1946, and from July to October, 1947. This species is unquestionably associated with human habitations and probably does not overwinter in the wild state.

Subgenus *Sophophora*

(1) *Melanogaster* group. Either *D. simulans* or *D. melanogaster* or both occurs in every locality at which more than one collection was made during the stated breeding seasons. It is of interest, however, to note that in no case was a single individual trapped prior to June 26 (the date of first occurrence in the Cambridge, Mass., area for 1947). Also in the Windham, Vermont, collection only one female was found in the middle of August. Evidently the season is so short at that locality, and the area is so isolated from any markets or stores that this group has a difficult time establishing itself in a wild environment. The town of Windham lies on the northeast side of one of the Green Mountains of Southern Vermont in the Canadian Life Zone and is evidently located in a region too severe for large expansion of the *melanogaster* group.

(2) *Obscura* group. Certainly three of the members of the *affinis* subgroup are found throughout this area and undoubtedly constitute a native population. These are *D. affinis, D. algon-*

quin, and *D. athabasca.* A few *athabasca* individuals were recorded in the Gray Gardens which might have proved to be *narragansett.* From the results of the small collections within the Canadian Life Zone it would appear that *D. athabasca* is the most successful species in getting established there: it was the most common species in the North Haven Island, Maine; the Vermont; and the Mount Washington collections. Probably *D. algonquin* holds an intermediate position between *D. athabasca* and *D. affinis* in regard to success in this area although it is possible that *D. algonquin* and *D. affinis* are about equal in their ability to withstand the adverse conditions of this region.

Subgenus Drosophila

(1) *Quinaria* group. Together with the *affinis* subgroup *D. quinaria, D. transversa,* and possibly a third species (as yet undescribed from this area intermediate between these two and strikingly similar to *D. subquinaria* in morphological characters) form what seems to be the principal native population of the genus in New England.

D. transversa is most common; it occurs in every collection in which more than one species was found. It accompanies *D. athabasca* into the Canadian Life Zone and is successful in all the regions in which *athabasca* is established. *D. quinaria* is much less common in all parts of the area; but possibly fewer *quinaria* come to banana traps than to other fruits like tomato for instance. Normal *D. quinaria* as described by Sturtevant was not obtained in any of the Vermont collections (although the numbers are so listed in the accompanying tables because of undecided classification). A smaller fly which is intermediate in color pattern between *quinaria* and *transversa* was present instead (four specimens). It is suggested that this intermediate form is a subspecies of *D. subquinaria* or a new species strongly resembling *D. subquinaria.* This type was also found in the Arnold Arboretum, Boston, and in the Gray Gardens, Cambridge. In the latter locality, however, normal *D. quinaria* was much more common (22 *D. quinaria* specimens and 3 *D. subquinaria* (?) specimens).

(2) *Testacea* group. *D. putrida* is about equal in numbers

of individuals to *D. transversa* among the native wild populations. This species occurs in almost every locality in which *transversa* and *athabasca* are found. There seems to be a slightly greater difficulty on the part of *putrida* in becoming established in colder regions or colder seasons of the year than in the case of the other two common species. Perhaps the figures are not too significant, but *putrida* is slightly less numerous than *transversa* in the Vermont collection; it is not found at all in the Maine island collection; and it is more warm-weather-loving in the Gray Gardens 1947 collections.

D. testacea is a rare fly which occurs in August in the Vermont collection and in summer and fall in Cambridge. The Vermont area may represent the borderline of its distribution region.

(3) *Melanica* group. Perhaps the most common and successful species of the genus in summer except for *melanogaster-simulans* is *D. melanica paramelanica.* This subspecies is rare in Vermont at the height of the summer, but it is very common in lower country.

D. nigromelanica, on the other hand, is quite rare even in the low regions. This species has been collected only around Boston.

(4) *Robusta* group. The last group which can be considered native is represented by *D. robusta* which occurs in small numbers in practically every locality. It is as common as *transversa* in Vermont where it can be found in deep forest of conifers, maple, and beech. It was especially common near small streams in the woods, showing that it prefers high humidity and cool conditions. It is somewhat less common near Boston where summer heat is more intense and woodland is not so dense. The 1947 collection was unexpectedly deficient in this species.

(5) *Funebris* group. *D. funebris* is not common in any locality and is quite spotty in distribution, having been found only in Vermont (one specimen) and around Boston.

(6) *Immigrans* group. *D. immigrans* accompanies *D. funebris* in the discontinuity and rarity of its occurrence. There can be no doubt that these two species do not overwinter in the wild state here, and they represent a small percentage of the

genus which is associated with man but breeds in small quantities during the summer in the wild.

(7) *Tripunctata* group. It was a surprise to discover *D. tripunctata* in the Gray Gardens in August and September, 1947. According to the latest distribution map (Patterson, 1943) it had never been recorded farther north than New Jersey. It is a fly of predominantly southern distribution, but it seems to breed here for two or three generations during the summer (Gray Gardens: Aug. 15, 2 specimens; Aug. 25, 1 specimen; and Sept. 18, 1 specimen).

(8) *Repleta* group. Because the writer was chiefly interested in obtaining flies in forested areas at some distance from human habitation, *D. repleta* was of rare occurrence. At any rate it was found only in collections near Boston, and is obviously not a wild species.

THE UNCLASSIFIED SPECIMENS IN THE QUINARIA GROUP

In May, 1946, a male specimen of this group and intermediate in many key characters between *D. transversa* and *D. quinaria* was found at the Arnold Arboretum, Mass. The specimen differed from ordinary male *quinaria* in the following characters: clouds on the apices of the second, third, and fourth longitudinal veins were absent; only two brown spots on tergite 6; and the lateral marginal spots on each tergite were nearly absent.

Later on in Vermont four females were obtained, which were of this intermediate type. No clouding at the apices of the longitudinal veins was observed; the abdominal tergite spotting was typical of *quinaria* in size except on tergite six where the spotting was variable, usually reduced in size in comparison with normal *quinaria*. The small lateral marginal spots typical of *quinaria* were greatly reduced or absent. Egg filaments were characteristic of *quinaria* rather than *transversa*. Male progeny from these females had only two spots on tergite six and no definite marginal spots at all. These males surprisingly had six or seven short recurved hairs on the median side of the fore-tarsus as described by Sturtevant (1942) for *D. subquinaria* rather than the long hairs in double row as in *D. quinaria*. Ordinary *D. quinaria* females were larger and darker in color

than these specimens. A few attempts were made to cross *quinaria* to the new type both in single pair matings and in mass matings of about five parents each. No fertile eggs were laid in any of the matings, but it is known to be difficult to raise *quinaria* by itself in the laboratory.

Some single pair matings of *D. quinaria* and of the new subspecies (or species) were made separately with interesting results: (1) In *D. quinaria* a few progenies lacked some or all of the clouding at the apices of the longitudinal veins; often reduction in size and number of abdominal tergite spots was encountered; that is, in females loss of lateral spots on the sixth tergite and in males loss of both these and the median spots. (2) In the progenies of the questionable specimens further reduction in spotting was quite common. Females often tend to lose all spots on the sixth tergite while males often showed a reduction or complete loss of lateral spots on the fifth tergite as well. This latter pattern is the common type of *D. transversa,* and shows that there is a possible breakdown here in the taxonomic characters.

If the difficulties involved in breeding these flies can be surmounted, it seems that a vast storehouse of easily recognizable morphological variation is involved in these species.

It is evident that we are dealing either with a new species or with an eastern subspecies of *D. subquinaria.* Since collecting has not been extensively carried on north of this area in New England heretofore, there remains the possibility that *subquinaria* occupies the Canadian region and extends down into the Canadian and Transitional Zones of New England. At any rate we do know that some members of the *affinis* subgroup do occupy the entire northern section of the country, and undoubtedly some members of the *quinaria* group accompany them. This supposition will merit further investigation, and the writer has reason to believe that specimens are not too rare for adequate collecting of this type or species in the future.

FLUCTUATIONS OF DROSOPHILA SPECIES POPULATIONS

For the breeding season of 1947 it was decided that sampling should be done for a single small area convenient to the laboratory at Harvard University. The Gray Herbarium Gardens

appeared to be the best site, and continuous collecting was carried on as often as possible from early April until late October. (The methods of sampling this area have been given previously.)

If we consider only the fluctuations in species populations of large enough size to be statistically significant, we can observe some rather interesting facts. Also a comparison of results for species with those obtained at the Aldrich Farm by Patterson (1943) shows some interesting parallels.

A graph has been constructed (see supplementary material) to show the maxima of each species during the season. In each

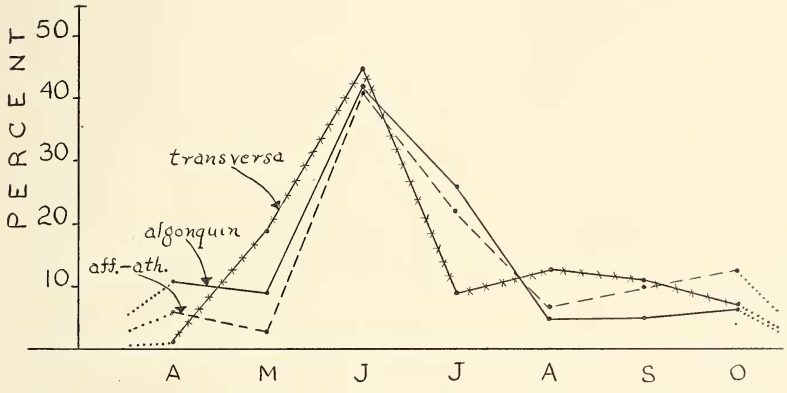

Figure 1. Gray Herbarium Gardens, Cambridge, Massachusetts, for 1947. This graph shows the fluctuations of those species whose maxima occur in the spring. Each point represents that per cent of the weighted number of specimens which was collected in that month (considering the total number for one species equal to 100 per cent.

species the data have been weighted to conform with the number of collections each month. Each point in the graph represents that per cent of the weighted number of specimens which was collected in that month (considering the total number for one species equal to 100%).

(1) The *affinis* subgroup together with *D. transversa* form a definite peak in June, then fall off for the remainder of the season. All of these species increase again slightly but not significantly as temperatures get cooler in late summer and early fall, but they fail to increase to their former proportions be-

cause other more aggressive species are then present in great number competing for space and food. The Aldrich Farm data for *affinis-algonquin* for 1939–40 show a very significant negative correlation with temperature (the writer has calculated r = –57.0 per cent. In New England too there is a very real preference in the *affinis* group and in *D. transversa* for mild temperatures. Temperature is apparently one of the most effective ecological factors in the distribution of these populations.

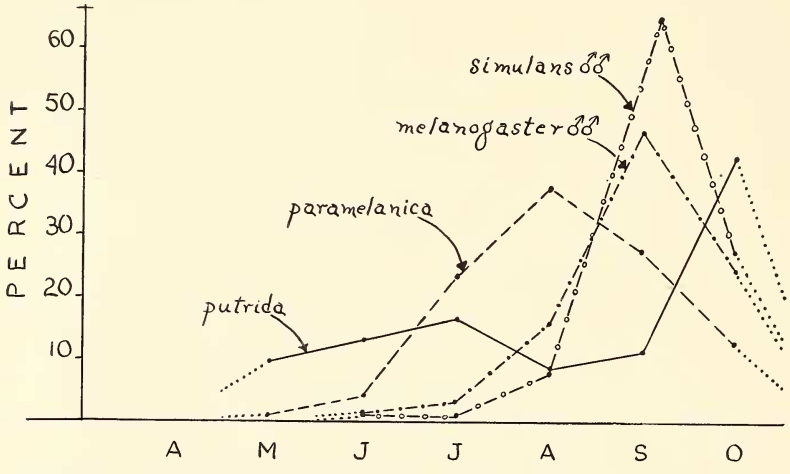

Figure 2. Gray Herbarium Gardens for 1947, showing the fluctuations of those species whose maxima occur in summer and early fall.

(2) During the month of July when temperatures average highest for the summer *D. putrida* attains a moderate peak; but probably this peak is not so much because of high temperature as because the previously dominant species have dropped considerably in numbers so that competition is effectively reduced. The fluctuations in size of *putrida* populations have always appeared somewhat enigmatical when compared with the weather data. Patterson (1943) has stated that some of the peaks of *putrida* in Texas coincide with rainfall peaks which in turn tend to increase fungus growth. However the writer has found no significant correlation between the rainfall data and the number of *putrida* specimens collected at the Aldrich

Farm. On the contrary the only significant correlation found from all the weather data given in the Patterson report was negative between humidity and number of specimens ($r = -64.3$ per cent). This correlation is more or less substantiated by the evidence here in New England: August was the most humid month but had the lowest number of *putrida* for the summer; October was an unusually dry month with exceptionally low rainfall, and *putrida* had its highest peak of the season. Probably *D. putrida* is a species which can increase in frequency when other species are not successful under dry conditions. It seems to be a mild temperature dry air fly; but when other more dominant species occur in the same environment, *putrida* is prevented from expressing much increase in size. It would appear from the accompanying graph that competition with larger species is a very important factor in the distribution of *putrida.*

(3) *D. melanica paramelanica* succeeds in forming an almost perfectly normal curve with its peak in August, the hottest month of the season. This species certainly follows the mean monthly temperature very well. Because it is a species which probably does overwinter in Boston and environs, it gets started early in the season and becomes well-established in the wild after the cool-loving species have dropped in frequency and just before the melanogaster-simulans complex becomes too numerous.

(4) No members of the *melanogaster* group were found until late June. As in the case of the Aldrich Farm collection *melanogaster* males appeared first to be followed by *simulans. Simulans* lagged slightly behind *melanogaster* for July and August but then formed a tremendous peak in September. Both species are quite significantly correlated with temperature in the Aldrich Farm data (the writer calculates $r = 79.0$ per cent), and unquestionably warm temperature is one of the chief ecological factors effecting a peak here in New England as well.

Considerable variation may possibly be encountered from year to year owing to changes in external conditions, but the pattern described here for this single seasons' fluctuations among the more prominent northeastern species will in general remain the same.

NEW ENGLAND COLLECTIONS—1946

Gray Herbarium, Cambridge, Mass.	July	August	September	Totals
No. of collections	4	1	4	9
D. affinis	9	0	6	15
D. algonquin	31	0	16	47
D. athabasca	6	1	30	37
D. busckii	8	0	0	8
D. immigrans	0	0	2	2
D. paramelanica	22	5	15	42
D. mel-simulans	21	10	88	119
D. nigromelanica	0	0	1	1
D. putrida	30	0	47	77
D. quinaria	4	0	0	4
D. robusta	7	0	4	11
D. testacea	1	0	0	1
D. transversa	20	0	9	29

NEW ENGLAND COLLECTIONS—1946

Arnold Arboretum, Boston, Mass.	April	May	June	July	Totals
No. of Collections	1	4	1	3	9
D. algonquin	1	1	1	2	5
D. immigrans	0	2	0	0	2
D. mel-simulans	0	0	0	3	3
D. putrida	0	6	1	14	21
D. quinaria	0	1	0	1	2
D. robusta	0	0	0	3	3
D. transversa	0	9	2	5	16

NEW ENGLAND COLLECTIONS—1946

Windham, Vermont	June	July	August	Totals
No. of collections	3	2	2	7
D. affinis	15	2	2	19
D. algonquin	0	1	3	4
D. athabasca	5	0	71	76
D. funebris	0	0	1	1
D. immigrans	0	1	0	1
D. mel-simulans	0	0	1	1
D. paramelanica	0	0	1	1
D. putrida	3	0	3	6
*D. quinaria**	3	1	0	4
D. robusta	5	5	3	13
D. testacea	0	0	2	2
D. transversa	5	3	5	13

* All individuals of this species in the Windham collection are atypical. See text.

New England Collections—1946

Braintree, Mass	July	August	September	Totals
No. of collections	3	1	2	6
D. algonquin	12	0	1	13
D. athabasca	23	2	13	38
D. funebris	0	1	0	1
D. immigrans	0	1	0	1
D. mel-simulans	20	41	40	101
D. nigromelanica	1	0	0	1
D. paramelanica	7	0	13	20
D. putrida	12	0	0	12
D. repleta	1	0	0	1
D. robusta	4	0	3	7
D. transversa	4	1	1	6

Northhaven Island, Penobscot Bay, Maine	June 23rd
D. algonquin	4
D. athabasca	46
D. transversa	1

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GRAY HERBARIUM COLLECTION—1947

	April	May	June	July	August	September	October
D. algonquin	44	13	147	90	14	18	14
D. athabasca	22	3	70	49	7	23	30
D. affinis	0	0	43	15	6	7	3
D. transversa	2	30	165	32	40	43	17
*D. quinaria**	0	1	4	12	3	3	2
D. putrida	0	25	78	99	44	76	173
D. testacea	0	0	4	0	9	2	4
D. funebris	0	6	16	0	1	1	1
D. paramelanica	0	2	33	206	298	273	50
D. nigromelanica	0	0	0	8	6	7	4
D. robusta	0	0	3	1	1	1	1
D. immigrans	0	0	0	1	2	15	10
D. busckii	0	0	0	4	8	9	11
D. tripunctata	0	0	0	0	3	1	0
D. repleta	0	0	0	1	0	0	0
D. melanog. ♂♂	0	0	1	15	71	262	83
D. simulans ♂♂	0	0	1	3	43	459	117
D. mel-sim. ♀♀	0	0	3	27	84	452	157
Totals **	68	80	568	563	640	1652	677
Number of Collections	11	4	9	9	8	10	6

* Includes three specimens of doubtful classification referred to in text.

** Total— ♂♂ = 2406.
♀♀ = 1843.

BOSTON WEATHER DATA—1947

	April	May	June	July	August	September	October
Temperature, F.							
Mean	47.2°	56.9°	65.4°	74.4°	73.2°	64.8°	61.6°
Maximum	75°	87°	89°	90°	99°	88°	89°
Minimum	30°	36°	46°	59°	54°	37°	38°
Greatest Daily Range	33°	33°	32°	22°	28°	29°	36°
Humidity							
Av. Rel.	65%	69%	70%	74%	78%	72%	71%
Precipitation							
Total	4.15″	4.36″	2.88″	3.98″	2.19″	3.95″	1.13″
Snow	0.60″	0	0	0	0	0	0

N.B. Maximum temperature for March was 58°, Average 37°

N. B. Maximum temperature for November was 59°, Average 41°.

Drosophila is very inactive at temperatures below 55° F. For all practical purposes the populations can be considered at 0 per cent for March and November. The first specimen of the season was collected on April 10, an *algonquin* female, although two collections had been made previously. The weather suddenly turned cold at the end of October and no collections were made in November.